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Spatial and Temporal Distribution and Overlap of Three Species of *Bullia* (Gastropoda, Nassariidae) on Exposed Sandy Beaches

by

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Abstract. Three species of plough shell, *Bullia rhodostoma, B. digitalis* and *B. pura,* coexist on dynamic sandy beaches in the Eastern Cape, South Africa. The robust *B. rhodostoma* is most abundant in the zone of swash and backwash, and exhibits great efficiency in foraging behavior, feeding on carrion stranded on the shore. The entire life cycle of this species is spent intertidally, while only adults of *B. digitalis* and *B. pura* appear on the beach, where they prefer a more subtidal habitat. The latter species exploit their surfing ability in the quest to capture food on its path shorewards and to migrate offshore during winter probably to spawn their eggs in deeper water. All three *Bullia* species move horizontally with the tides, a behavior facilitating continuous access to food. Although zonation is evident among the three whelk species, some spatial overlap exists. *Bullia rhodostoma* is the most widely distributed while *B. digitalis* shows the greatest overlap with the other two species.

INTRODUCTION

THE EXPOSED SANDY BEACH, despite little spatial heterogeneity and much physical instability, harbors a marine fauna of some ecological diversity. Eighteen species have been recorded in the Eastern Cape, South Africa, with four mainly intertidal forms constituting 99.5% of the biomass. The plough shell *Bullia rhodostoma* Reeve, 1847, makes up 1.7%, while the other two species, *B. digitalis* (Dillwyn, 1787) and *B. pura* Melvill, 1885, account for only 0.4% of the total biomass. The large white sand mussel *Donax serra* Botten, 1848, dominates the macrofauna comprising 97.3%, while the smaller mussel *D. sordidus* Hanley, 1845, contributes only 0.1% of the biomass (Mc Gwynne, 1980; Mc Lachlan *et al.,* 1981).

Although their contribution to the macrofaunal biomass is small, the ecological importance of *Bullia* is indicated by their abundance (particularly *B. rhodostoma*) and their position in the food chain (Brown, 1964, 1971). Snails of *B. rhodostoma* with shell lengths ranging from 3 to 52 mm have been recorded (Mc Lachlan *et al.,* 1979a) while a much narrower size range has been encountered in both *B. pura* (11–29 mm) and *B. digitalis* (22–42 mm) (Mc Gwynne, 1980). The snails function as predator/scavengers, feeding on a wide range of organisms stranded in the swash. The most important predator of *Bullia* is the swimming crab *Ovalipes* (Du Preez, 1981). The holocephalan *Callorhynchus,* elasmobranch *Rhinobatus,* and teleosts *Coracinus, Lithognathus* and *Rhabdosargus* prey on the plough shells during high tide. The sanderling *Crocethia* feeds on *Bullia* while they are exposed at low tide (Mc Lachlan *et al.,* 1981; Brown, 1982).

Brown described the mode of life of *Bullia* on beaches in the Western Cape and conducted extensive research into their ecophysiology. Recently, Brown (1982) reviewed the existing knowledge on the biology of *Bullia* in South Africa. In the Eastern Cape, the general ecology of *B. rhodostoma* has been described (Mc Lachlan *et al.,* 1979a, 1979b) and aspects of the physiology of the genus recorded (Ansell & Mc Lachlan, 1980; Dye & Mc Gwynne, 1980; Mc Gwynne, 1980; Mc Lachlan & Young, 1982).

On beaches in the Eastern Cape, *Bullia rhodostoma, B. digitalis,* and *B. pura* appear to coexist in a relatively unstructured habitat where little niche differentiation is evident. The aim of this paper is to describe aspects of the ecology of only the latter two species, such as distribution and abundance, and to determine how the three whelk species apparently coexist successfully in the "uniform" environment of the sandy beach.

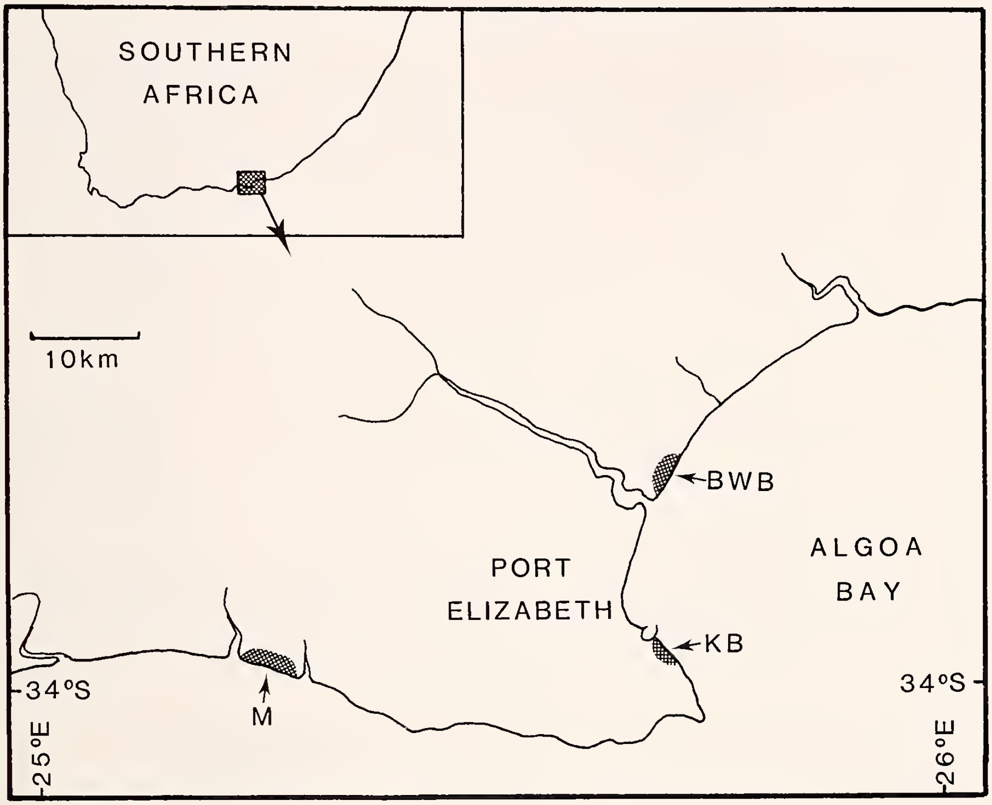

Figure 1

Map of Southern Africa, showing the locations of the three study beaches: Maitlands (M), Kings (KB) and Bluewaterbay (BWB).

THE STUDY AREA

Three beaches were selected as study sites (Figure 1). Maitlands beach is a southfacing beach lying 30 km west of Port Elizabeth; Kings beach and Bluewaterbay beach face northeast and east, respectively, into Algoa Bay. The main features characterizing the three beaches have already been described by Mc Lachlan (1977, 1979) and are summarized in Table 1. These represent average conditions, which may differ markedly during extreme calm or storms.

Maitlands beach supports a high macrofaunal biomass. The total ash-free dry biomass approaches 7 kg/m of shoreline (Mc Lachlan *et al.,* 1981), the major contributor being the large white sand mussel *Donax serra.* Less common inhabitants of the beach zone include the swimming crab *Ovalipes,* sand-burrowing mysid *Gastrosaccus,* and isopods, chiefly *Eurydice. Donax serra* is absent on Kings beach and present in low numbers on Bluewaterbay beach. Populations of beach macrofauna on the latter two beaches are much smaller than on the high energy beach at Maitlands.

METHODS

Distribution and Abundance

Sampling of *Bullia digitalis* and *B. pura* was conducted approximately every six weeks from January 1978, to December 1979, on Maitlands beach, and from January to December 1979, on Kings and Bluewaterbay beaches. A dredge (0.5 m wide with 1.5-mm mesh) was used to complete a series of five hauls for each sample. Each haul was 10 m long and cut 5 cm into the sand; thus, a 25-m^2 area was sampled. The hauls were continuous, with no overlap between each haul. The sampling procedure covered a 50-m line from a point 5 m below LWS (low water springs) to just above the mean tide level. This was essential as *B. digitalis* and *B. pura* inhabit deeper water than the intertidal resident, *B. rhodostoma.*

The appearance of *Bullia rhodostoma* in dredged samples was ignored, as its distribution and abundance has already been described (Mc Lachlan *et al.,* 1979a). The occurrence of this species was, however, noted in five samples taken from Maitlands beach from April to October 1979, to measure the degree of overlap in the distribution

Table 1

Characteristic features of the three East Cape beaches, Maitlands (M), Kings (KB), and Bluewaterbay (BWB).

Feature	Maitlands	Kings	Bluewaterbay
Average slope of beach	gentle $\frac{1}{33}$ concave	moderate $\frac{1}{25}$ concave	steep $\frac{1}{20}$ concave
Average width of intertidal	100 m	50 m	40 m
Width of surf zone	150–400 m	30–120 m	50–200 m
Swash periods	20–30 sec	10–23 sec	12–20 sec
Wave periods	14 sec	10 sec	10 sec
Volume of seawater filtered through interstices (m^3/m/day)	9	7	12
Grade of sand	very well-sorted medium quartz particles	clean fine well-sorted quartz	well-sorted fine to medium quartz sand with large shell fragments and pebbles around LWS
Particle size range (median diameters)	268–308 μm	200–220 μm	variable size, median 250 μm
General appearance	Gentle sloping beach backed by extensive dune system. Strong wave action.	Berm present 2 m above LWS, dunes poorly developed. Moderate wave action.	Berm 1.25 m above MTL, dunes poor. Wave action moderate to strong.

of the three beach populations. All animals collected were measured to 1 mm greatest shell length using vernier callipers.

Due to the absence of juvenile snails of both *Bullia digitalis* and *B. pura* from the beach zone, sampling was extended into the offshore region beyond the breakers. A dredge 0.33 m wide with a mesh size of 4 mm was dragged by a motorboat and guided by a diver using SCUBA. The series of hauls was approximately 10 m in length and in water depths ranging from 3 to 8 m.

Tidal Migrations

The tidal movements of *Bullia digitalis* and *B. pura* were monitored during spring tides in March and again in November 1979. Mc Lachlan *et al.* (1979b) recorded the tidal migrations of macrofauna resident in the intertidal zone just below ELWS to EHWS (extreme low water springs, extreme high water springs). Preliminary observations showed *B. digitalis* and *B. pura* to prefer a more subtidal habitat than the intertidally dominant *B. rhodostoma.* During March of this study, the sampling zone was extended from ELWS seawards to the line of breakers initiating the dynamic surf zone. In November, the first line of breakers marked the seaward extent of the sampling procedure. Steel rods, at 20 m intervals, marked each sampling site. A second series of rods, 10 m from and parallel to the first, marked the length of each strip of beach to be dredged. Samples were taken every 3 h for 12 h over two tidal cycles using the smaller 4-mm mesh size dredge. No area was sampled more than once in 6 h. The dredge proved to be efficient on dry sand and at water depths to approximately 4 m.

Niche Breadth and Overlap

In terms of the spatial model of the niche by Hutchinson (1958), niche breadth is the "distance through" the niche along some particular line in niche space. The distribution of whelks on the beach was taken to represent this line, and its vertical range and evenness of spread were calculated using an index of niche breadth, B. We used data collected at Maitlands beach over five months (from April to October 1979) when all three species were sampled through a series of five tidal levels. Numbers collected in 5-m^2 dredged samples at each level were used to calculate the following quantity:

$$B = \frac{1}{\sum_{i=1}^{n} P_i^2}$$

where B is the niche breadth of a species, P_i is its proportion (in numbers) in the *i*th habitat unit of the environment, and *n* is the number of units. The sandy beach was the habitat and the series of five dredges taken each month made up the units. The index was calculated for each species for every month over the five-month period. The theoretical maximum niche-breadth value was estimated by assuming an even distribution of the three species over the five units.

Niche overlap is simply the joint use of a resource by two or more species. As in niche breadth, the resource is space. Niche overlap is calculated as:

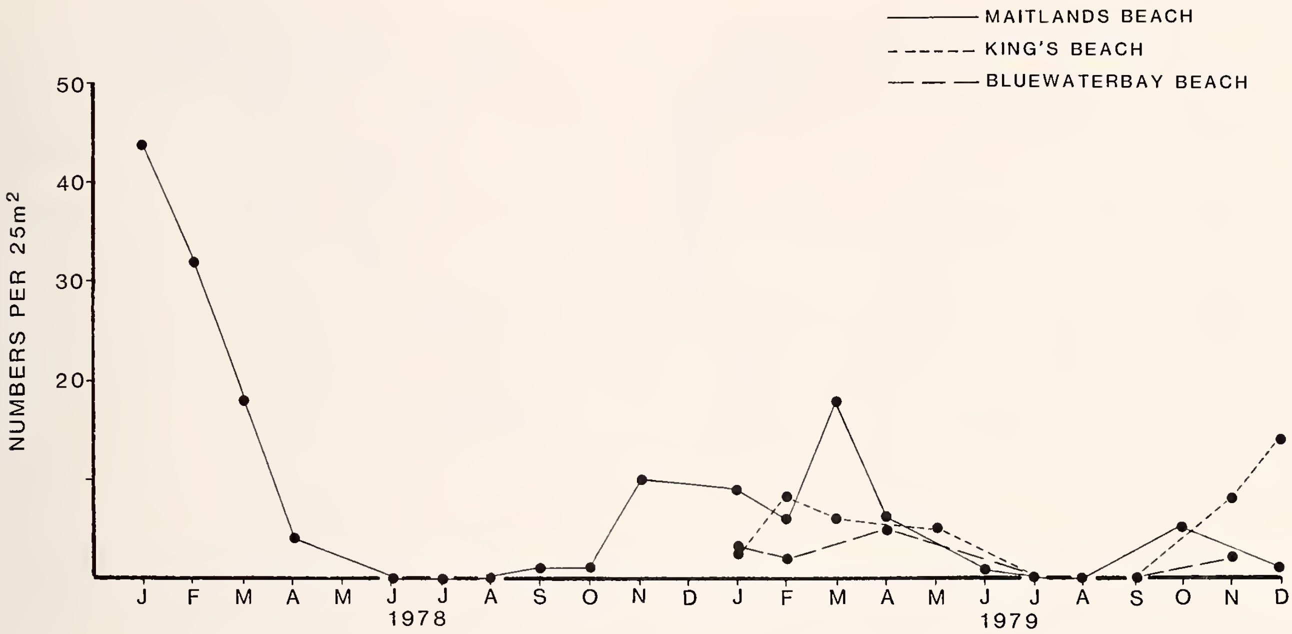

Figure 2

Temporal abundance of *Bullia digitalis* on three beaches in the Eastern Cape, South Africa.

$$\alpha_{jk} = \frac{\sum_h P_{jh} P_{kh}}{\sum_h P_{jh}^2}$$

where α is the niche overlap or probability of species k overlapping species j, and P_{jh} and P_{kh} are the proportions of species j and k respectively in the hth unit of the habitat. If the distribution for the two species is identical (*i.e.*, complete overlap), $\alpha = 1$ (LEVINS, 1968). Interspecific niche overlaps were calculated monthly and estimated for the overall sampling period.

RESULTS

Temporal Abundance and Distribution

Two peaks of abundance were evident for both *Bullia digitalis* and *B. pura* on all three beaches (Figures 2, 3). Maximum densities of *B. digitalis* occurred during midsummer (November to January) with a smaller peak in and around March. *Bullia pura* was most numerous in December and January, and then again during March and April. Numbers of both species were low, reflecting the absence of juvenile snails. No distinct year classes were discernible. Snails appeared to be patchily distributed in groups. The sampling procedure, and probable inefficiency of the dredge, did not always reflect the true distribution and abundance patterns on the beach.

The samples containing *Bullia rhodostoma* show this population to occur intertidally and higher on the shore than *B. digitalis* and *B. pura,* which were confined to lower tidal levels and deeper waters.

The offshore hauls located juvenile snails of both *Bullia pura* and *B. digitalis* coexisting with juveniles of four other *Bullia* species, namely *B. callosa* Wood, 1828, *B. annulata* (Lamarck, 1816), *B. laevissima* (Gmelin, 1791), and *B. tenuis* Gray, 1839. Notable differences in shell morphologies eliminated confusion over their taxonomic identity. A t-test indicated a significant difference in the mean shell lengths between the beach and offshore populations of *B. digitalis* ($P < 0.005$) and *B. pura* ($P < 0.005$). Two other gastropods, *Ancilla albozonata* Smith, 1904, and *Melapium lineatum* (Lamarck, 1822), were also found in the deep-water samples.

Tidal Migrations

Figures 4 and 5 show the profile of Kings beach along with the pattern of tidal migration undertaken by the whelks during both monitoring sessions. Only the spatial ranges and not changes in abundance of the snails are shown. One snail in a dredged sample was taken as representative of the presence of a species at a particular location and time. Despite low numbers, migration patterns on both occasions revealed similar trends. All three species showed distinct movements with the tides. *Bullia rhodostoma* kept abreast and sometimes slightly ahead of the incoming swash, while *B. pura* and *B. digitalis* failed to penetrate the swash, always remaining in deeper water.

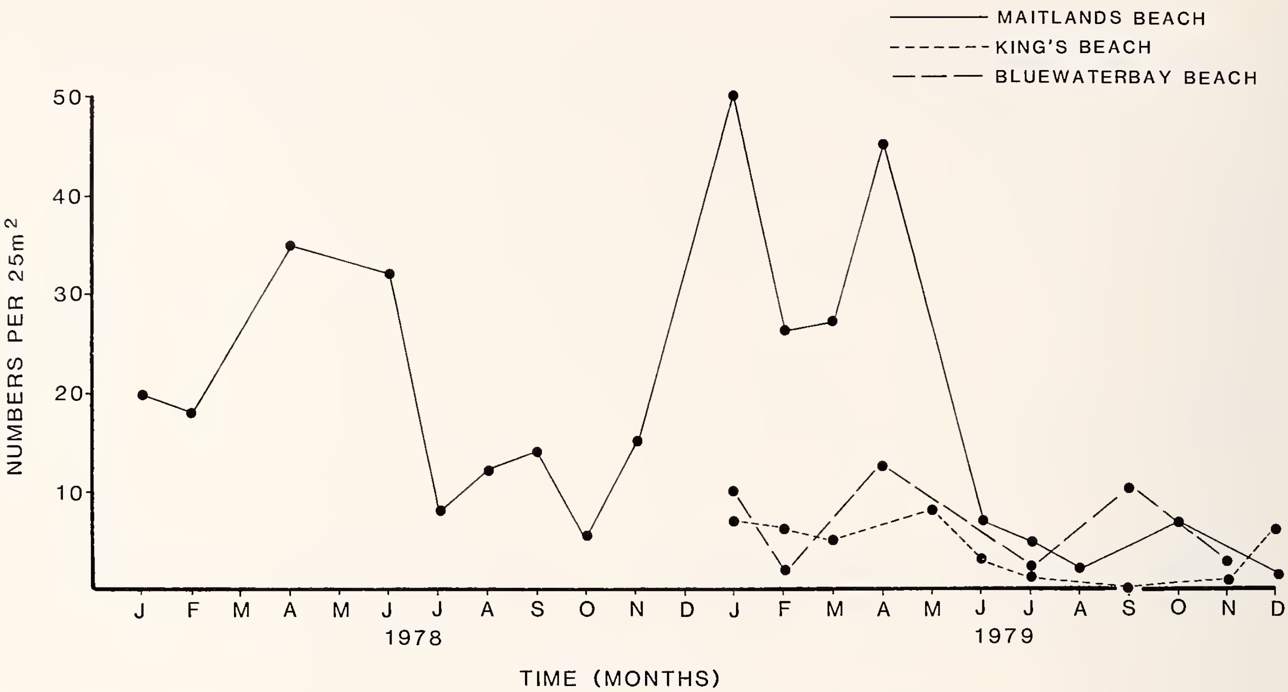

Figure 3

Temporal abundance of *Bullia pura* on the three South African East Cape beaches.

Bullia pura, however, extended into shallower water than *B. digitalis.*

Niche Breadth and Overlap

Numbers of *Bullia digitalis* and *B. pura* collected were generally low and fluctuated over the sampling period (Table 2), while numbers of *B. rhodostoma* increased steadily towards October. *Bullia digitalis* was absent during mid-winter (July–August) and numbers of *B. pura* declined over this period. B values were all under 5, the theoretical maximum that would indicate a uniform distribution of snails throughout the study area. The greatest niche breadth was recorded in *B. rhodostoma* for October, the value reaching 78% of the maximum. Niche breadths of *B. digitalis* and *B. pura* proved variable, ranging from 0 to 3.5. Calculation of the overall B for each species showed *B. rhodostoma* to be the most widespread population, with *B. pura* confined to the narrowest zone. Interspecific zonation is suggested by the average B values (Table 3), as these never reach 60% of the value indicative of an even distribution.

The greatest species overlap occurred between *Bullia rhodostoma* and *B. pura* (Table 4) particularly during April and October. Overlap between each of the former species and *B. digitalis* was negligible, except for October when the overlap proved noteworthy. *Bullia digitalis* and *B. pura* populations overlapped markedly when both species were present on the shore.

DISCUSSION

Distribution

The same basic pattern of distribution appeared on all three sandy beaches. *Bullia rhodostoma* occupied a broad band of the intertidal, whereas the adults of *B. digitalis* and *B. pura* restricted themselves to the subtidal, the juveniles remaining offshore beyond the breakers. Mc Lachlan *et al.* (1979a) recorded a size-based zonation at low tide, with the smaller snails situated uppermost on the shore. The effect of shell length on distribution patterns was not measured in this study.

On Muizenberg beach in the Western Cape, Brown (1971) found snails of *Bullia rhodostoma* and *B. digitalis* occurring in well-defined groups of a single species within a narrow size range. No vertical pattern of zonation was noted. He attributed this distribution to a sorting process promoted by wave action. Mc Gwynne (1980) demonstrated that *B. rhodostoma,* aided by a large foot and a light shell, surfed at a faster rate than the other two species. Both *B. digitalis* and *B. pura* have smaller feet and heavier shells, which enable them to withstand current surges more effectively than *B. rhodostoma* and, thus, maintain their subtidal position on the shore. The physical characteristics of *B. rhodostoma* also promote speed and efficiency in crawling on wet sand, essential attributes for this species to reach carrion stranded in the swash. *Bullia digitalis* and *B. pura* are not equipped to compete with *B. rhodostoma*

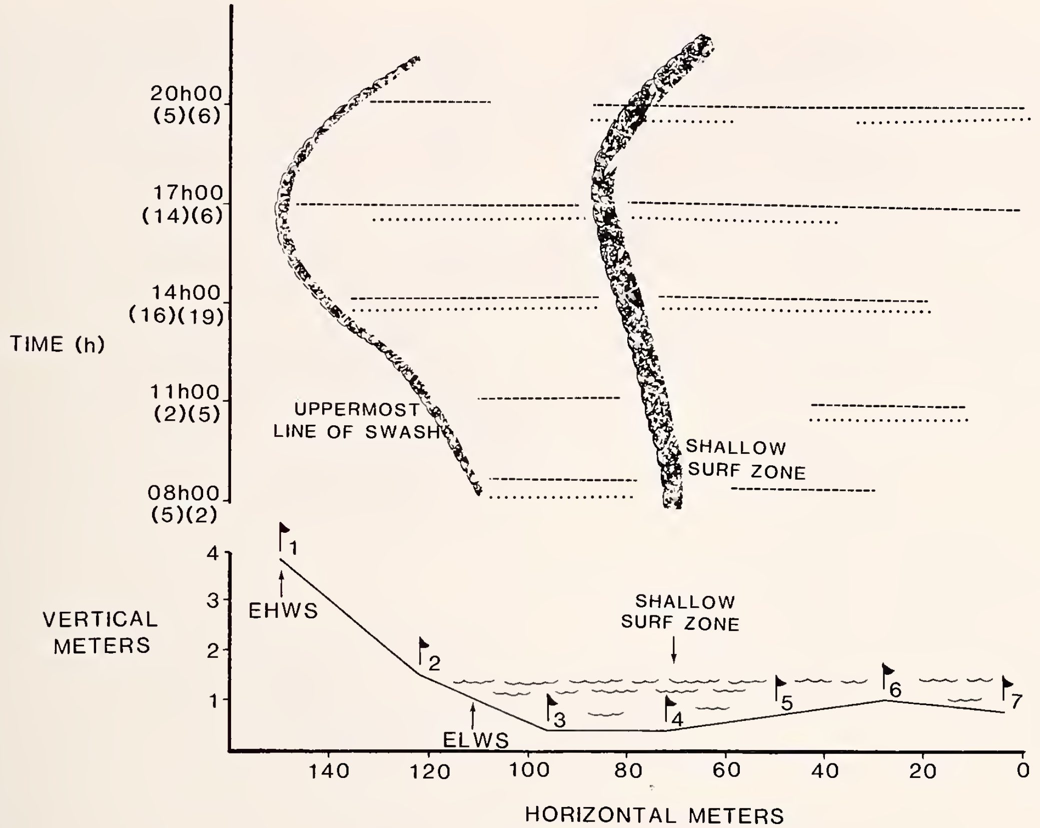

Figure 4

The migration patterns of beach populations of *Bullia pura* (– – –) and *B. digitalis* (· · · · ·) during a spring tidal cycle in March 1979. Actual numbers of each species caught in the dredge at each sampling time are shown in parentheses below the time scale on the vertical axis. The profile of Kings beach is also shown.

in this pursuit and probably exploit different feeding strategies subtidally in their quest for food and, therefore, survival.

In experiments correlating the distribution of *Bullia digitalis* with the grade of sand on west coast beaches, Brown (1961) and Bally (1981) showed this species to prefer no particular sediment. At Bluewaterbay beach in Algoa Bay, a series of dredge hauls from the beach towards and along the mouth region of the Swartkops River indicated the presence of *Bullia* until a point where the ripple effect of waves became negligible. This coincided with an increase in the slope of the river bank. During the hauls, there was no marked change in either sediment grade or salinity of seawater. A combination of the effects of wave action, water currents, and beach slope could act as factors limiting the distribution of the snails.

Abundance

The absence of juveniles of both *Bullia digitalis* and *B. pura* from the beach and their appearance in offshore dredged samples suggest that the egg-laying females migrate to deeper, less turbulent waters to deposit their egg capsules. This presumed offshore migration could account for the decrease in the beach populations of *B. pura* during January and February and *B. digitalis* from February to April. Eggs of *B. rhodostoma* are spawned in mid-summer (December/January) (Mc Lachlan *et al.*, 1979a) at the same time as those of *B. pura,* but slightly before *B. digitalis* (Mc Gwynne, 1980).

The entire population of *Bullia digitalis* moves offshore during the winter, while snails of *B. pura,* although few in number, are always found on the beach. This may be related to the apparently seasonal occurrence of carrion (Mc Gwynne, 1980) and the possible presence of a more constant food supply in deeper waters in winter. *Bullia digitalis* has been found at depths exceeding 20 m (Brown, 1982) along the west coast, particularly off exposed beaches with steep slopes.

Snails of both species return in late spring to early summer to the shallows. Copulation takes place then, with the males exploiting the mobility of the swash to find mates. Females remain on the beach for about two to three

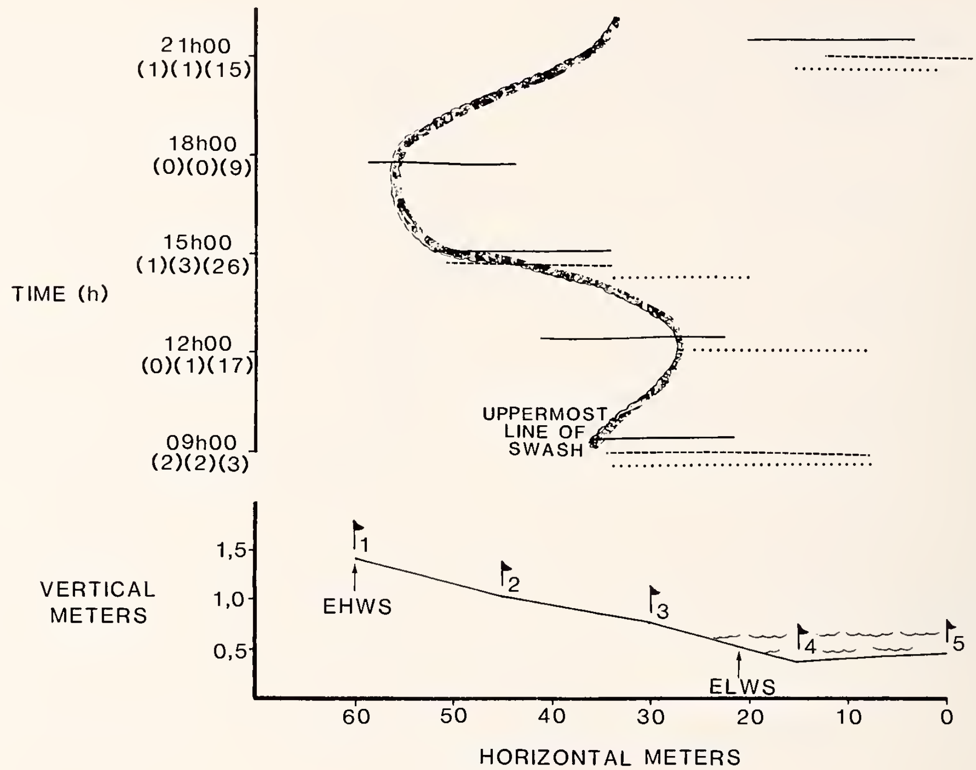

Figure 5

Migrations undertaken by beach populations of *Bullia pura* (– – –), *B. digitalis* (·····), and *B. rhodostoma* (——) during a spring tidal cycle in November 1979. Actual numbers of each species caught in the dredge at each sampling time are shown in parentheses below the time scale on the vertical axis. The profile of Kings beach is also shown.

months after copulation, with the sperm presumably stored. The second peak of abundance of *Bullia digitalis* and *B. pura,* in March and April, respectively, could indicate the return of the females to the beach after depositing their egg capsules offshore.

Tidal Migrations

All three *Bullia* species migrate with the tides, differing in the extent of their vertical penetration. *Bullia rhodostoma,* located higher on the shore than *B. digitalis* and *B. pura,* is carried with the swash and often stranded above

Table 2

Numbers of *Bullia rhodostoma* (Br), *B. digitalis* (Bd), and *B. pura* (Bp) at five beach sites, each 4 m², from the swash (site no. 1) to water of approximately 1 m deep (site no. 5). B = niche breadth.

	April			June			July			August			October		
Site no.	Br	Bd	Bp	Br	Bd	Bp	Br	Bd	Bp	Br	Bd	Bp	Br	Bd	Bp
5	0	1	1	2	1	0	6	0	1	1	0	1	0	2	0
4	0	3	1	0	1	2	3	0	0	9	0	1	32	2	0
3	0	2	11	4	0	2	2	0	3	3	0	1	24	1	3
2	5	1	13	10	0	3	17	0	0	2	0	0	41	0	0
1	12	0	20	19	0	1	22	0	1	50	0	0	40	0	4
Total	17	7	46	35	2	8	50	0	5	65	0	3	137	5	7
B	1.7	3.2	3.1	2.5	2.0	3.5	3.0	0.0	2.7	1.6	0.0	3.1	3.9	2.7	1.9

Table 3

Niche breadth values, B, calculated for each species.

Species of *Bullia*	Total B over all months	Average B	% B of theoretical maximum
B. rhodostoma	0.46	2.5	50
B. digitalis	0.87	1.6	32
B. pura	0.53	2.9	58

the tide, where it forages in search of stranded carrion. The latter two species are carried up the beach with waves on the incoming tide, and burrow rapidly into the sand as the velocity of the incoming wave diminishes.

ANSELL & TREVALLION (1969), working on *Bullia* species on the Indian coastline, found the changing velocity of the backwash of the ebbing tide to be the critical factor in the emergence and subsequent movement back to deeper water of these snails.

Bullia digitalis and *B. rhodostoma* on west coast beaches occupy the same intertidal position (BROWN, 1971). Here, they kept pace with the tides during low and mid-water, emerging occasionally in the saturated foreshore to feed; they always remained buried at high water. On east coast beaches, *B. digitalis* (and *B. pura*) maintains a subtidal position, probably feeding on dead-animal remains washing back and forth in the waves. It has not been seen foraging in the manner of the west coast species (MC GWYNNE, 1980). The movements of the plough shells over a large part of the intertidal zone give them access to food in a wider area than if they remained fixed at one tidal level.

Niche Breadth and Overlap

Niche breadth indices suggest some spatial partitioning between the three *Bullia* species on the shore. Dredging

Table 4

Niche overlap (α) between each of the three intertidal *Bullia* species over the period from April to June 1979. Br = *B. rhodostoma*. Bd = *B. digitalis*. Bp = *B. pura*.

Species overlapping/ species overlapped	Niche overlap (α)[a]					
	April	June	July	August	October	Overall
Br/Bd	0.14	0.06	0.00	0.00	0.35	0.17
Bd/Br	0.07	0.08	0.00	0.00	0.49	0.09
Br/Bp	1.20	0.72	0.36	0.20	0.46	0.54
Bp/Br	0.65	0.53	0.41	0.11	0.92	0.47
Bd/Bp	0.37	0.43	0.00	0.00	0.16	0.17
Bp/Bd	0.38	0.25	0.00	0.00	0.23	0.28

[a] The values indicate the probability of one species overlapping the other with the species being overlapped read as the denominator.

covered only an area from the swash line to a water depth of approximately 1 m. The niche breadth and overlap analyses, therefore, only indicate spatial niches in the shallow zone of swash sampled, and do not reveal the total dominance of the upper intertidal by *B. rhodostoma* or the absence of this species from deeper waters. The niche indices also give no indication of the competitive interactions involved in the partitioning of food between the three whelk species, the access to which is vital for their survival on the beach.

The offshore migrations presumably undertaken by *Bullia digitalis* and *B. pura* would obviously reduce spatial overlap between all three species and increase their niche breadths. The species diversity and population dynamics of deep-water macrofauna have not been measured. The area beyond the breakers remains relatively unexplored.

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